

Another variation on the gymnure theme: description of a new species of *Hylomys* (Lipotyphla, Erinaceidae, Galericinae).

PAULINA D. JENKINS

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD

MARK F. ROBINSON

Waterway Conservation & Regeneration, British Waterways, Llanthony Warehouse, Gloucester Docks, Gloucester, GL1 2EJ

SYNOPSIS. A new species of *Hylomys* from Lao Peoples Democratic Republic is described, based on morphological comparisons with other members of the subfamily Galericinae. The relationships revealed by a phylogenetic analysis are discussed and compared with those of a previous published analysis.

INTRODUCTION

The Family Erinaceidae is divided into two subfamilies: the widespread Erinaceinae (hedgehogs) occurring in Africa, Europe and Asia, and the Galericinae (moonrats and gymnures), which is confined to southeast Asia, Indonesia and the Philippines. There has been considerable disagreement over the correct name to apply to the subfamily of moonrats and gymnures, summarised by Frost *et al.* (1991), who favoured the use of Hylomyinae. McKenna & Bell (1997) pointed out however, that the use of Galericipini as a tribal name by Butler (1948) had been accepted by many subsequent writers, particularly palaeontologists, and was therefore the appropriate name to use. In this paper we follow McKenna & Bell (1997) in using the name Galericinae. Most authors up to and including Corbet (1988), considered that the Galericinae includes five genera: *Echinosorex* Blainville, 1838, *Hylomys* Müller, 1840, *Neotetracus* Trouessart, 1909, *Neohylomys* Shaw & Wong, 1959 and *Podogymnura* Mearns, 1905, all but the latter being monotypic. In their revision of the family Erinaceidae, Frost *et al.* (1991) concluded that there are only three valid genera within the Galericinae: *Echinosorex*, *Podogymnura* and *Hylomys*. They accepted *Hylomys* as a rather variable but nevertheless monophyletic genus, although they conceded that there was evidence to support the retention of *Neotetracus* and *Neohylomys* as subgenera.

The genus *Hylomys* is widely distributed in southeast Asia and Indonesia. *Hylomys suillus* Müller, 1840 occurs in Malaysia, Indonesia, Thailand, Vietnam, Cambodia, Lao Peoples Democratic Republic (PDR), Myanmar and southern PDR China; in Lao PDR it has been recorded from Phongsali, Xiangkhouang, Vientiane and Dong Hua Sao National Biodiversity Conservation Area (NBCA) (Robinson, 1999). A number of different subspecies have been attributed to *H. suillus* and the biochemical and metrical variation within this species was examined by Ruedi *et al.* (1994). They recognised that much of the high level of variation could be attributed to the geographical and altitudinal isolation of the named forms but demonstrated that one of these taxa, *H. parvus* Robinson & Kloss, 1916, merited specific status. *Hylomys sinensis* (Trouessart, 1909) occurs from southern China to Myanmar and northern Vietnam; it has not been recorded from Lao PDR but is likely to occur in those areas adjacent to northern Vietnam, whence it is recorded by Osgood (1932). *Hylomys hainanensis* (Shaw & Wong, 1959) is

restricted to Hainan Island, PDR China and *H. parvus* is known only from Sumatra, Indonesia. Another geographically isolated undescribed gymnure has been discovered recently from a region of limestone karst in the Lao PDR. While sharing many characters with other species of *Hylomys* this new species also differs markedly from its congeners and, furthermore, shares some features with geographically remote species of *Podogymnura*. The new taxon has been compared in particular with specimens of *H. suillus*, although there is no indication that the two species occur sympatrically, and also with *H. sinensis*, *H. parvus* and, in the absence of specimens, with the original description of *H. hainanensis* and the figures of the skull of this species in Frost *et al.* (1991). In addition comparisons were made with the other genera of Galericinae: *Echinosorex gymmura* (Raffles, 1822) from Malaysia and Indonesia, and *Podogymnura truei* Mearns, 1905 from the Philippines. In order to assess phylogenetic relationships, both the new taxon and *H. parvus* were analysed using the criteria employed by Frost *et al.* (1991).

MATERIAL AND METHODS

Comparative material was examined from the collections of the Natural History Museum (BMNH), London (formerly the British Museum (Natural History)), the American Museum of Natural History, New York (AMNH), the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Thailand Institute of Scientific and Technological Research, Bangkok (TISTR), as listed in Table 1.

All measurements are in millimetres and were taken using digital calipers. Cranial and dental nomenclature follows Butler (1948), Novacek (1986), Frost *et al.* (1991) and Gould (1995). Dental notations are indicated in the text in the following manner, with premaxillary and maxillary teeth denoted by uppercase letters and mandibular teeth by lowercase: incisor (I/i), canine (C/c), premolar (P/p), molar (M/m), thus P3 refers to the third upper premolar, i2 to the second lower incisor.

PHYLOGENETIC ANALYSIS

Cranial, dental, skeletal and external characters were scored for the new species and *H. parvus* according to the character transformation

series employed by Frost *et al.* (1991: 3–15) and added to the character matrix shown in Frost *et al.* (1991: appendix 2) see Table 2. Branch and bound analyses were performed using Paup 4.0ba (Swofford, 1999) set at maximum parsimony, with a maximum trees setting of 1000 and all characters treated as unordered and of equal weight. Bootstrap analyses (Felsenstein, 1985) were made to provide an assessments of confidence limits of nodes, with 1000 replicates of 100 random addition sequence replicates. Bremer support indices were calculated by increasing the upper bound of the shortest tree by one step, repeating the branch and bound analysis and producing a strict consensus tree; the process was repeated, progressively increasing the length of the suboptimal cladograms by a single step until all clades of interest no longer occurred on the consensus tree; the level at which each node collapsed was recorded (Kitching *et al.*, 1998). Both accelerated (ACCTRAN) and delayed (DELTRAN) optimizations were used to map character evolution. The trees obtained were compared with those in Frost *et al.* (1991) and the results of the analysis are given below.

RESULTS

Hylomys megalotis, sp. nov.

HOLOTYPE. BMNH 1999.44 (field number 5/99) male, body in alcohol, skull extracted. Collected 15 January 1999 by M. F. Robinson.

TYPE LOCALITY. Environs of Ban Muang and Ban Doy, c 18 km North of Thakhek, Thakhek district, Khammouan Limestone National Biodiversity Conservation Area, Khammouan Province, Lao Peoples Democratic Republic, 17°33'15"N 104°49'30"E. Habitat: steep slopes around the base of massive limestone karst, covered in rock and large boulders, with an underlying soil base and heavily degraded mixed deciduous forest, scrub and bamboo. Low lying areas away from the karst had been cleared for cultivation of paddy rice.

PARATYPES. BMNH 1999.45 (field number 14/99) collected 16 January 1999; 1999.46 (field number 15/99) and 1999.48 (field number 17/99) collected 17 January 99, females, bodies in alcohol, skulls extracted; 1999.47 (field number 16/99) collected 17 January 1999, male, skin and internal organs in alcohol, skull and skeleton. All specimens were collected by M.F. Robinson from the same locality as the holotype.

DIAGNOSIS

Ears large, rhinarium elongated; first and fifth digits of forefeet long, claws long, cheiridia large and rounded; cheiridia on hindfeet large, soles naked; pre-anal gland with single opening. Skull with posterior region of nasals extending to level of antorbital rim; maxilla and parietal widely separated by frontal in supraorbital region; long grooves for palatine artery present in palate; anterior palatine foramina anterior to maxillary palatine suture; antorbital fossa shallow; nasolabialis fossa shallow; posteroventral maxillary process of zygoma distinct; antero-ventral process of alisphenoid present. Dentition robust. Third upper premolar (P3) large with well developed lingual cusp and three roots. Neural spine of axis low.

DESCRIPTION

Medium sized *Hylomys* with a long tail, approximately 75% of head and body length. Pelage grey, long, soft and very fine, lacking flattened spinous hairs; individual hairs grey for most of their length, then buff with buff or black tips. Dorsal region of rhinarium narrow, elongate posteriorly; ears prominent, very large, rounded. First and

fifth digits of forefeet lengthened, claws long and moderately stout; sole and tarsal region of hindfeet naked, cheiridia large. Pre-anal gland with single opening immediately posterior to cloaca. Two pairs of inguinal mammae present.

Skull elongate, moderately slender and somewhat flattened in appearance (see Figs. 1–2); dorsal profile more or less straight, showing a gradual increase in height from anterior of rostrum to braincase. Rostrum long, slender and moderately shallow, nasals long extending posteriorly to, or slightly beyond, level of antorbital rim; posteroventral region of premaxilla widely separated from anterodorsal region of frontal by maxilla; interorbital region moderately narrow; supraorbital processes of frontals scarcely evident; frontals anteriorly depressed in midline; supraorbital region of frontals broad, so that the maxillaries are widely separated from the parietals; parietals extend anteriorly in supraorbital and orbital region but do not form an anterior process; supraorbital foramen present in dorso-orbital region of frontals; orbital region of maxilla broad, forming major portion of the anterior region of the orbit; orbital region of frontal constricted anteriorly by maxilla, posteriorly by parietal; orbitosphenoid anteroposteriorly expanded, optic foramen posteromedially positioned, anterodorsal to, and moderately well separated from, the suboptical foramen and from the ethmoid foramen (see Fig. 3); crest present leading from anterior alisphenoid diagonally across orbitosphenoid, partially obscuring optic, suboptic and sphenorbital foramina in lateral view; alisphenoid dorsoventrally compressed, fusiform anteroventral process of alisphenoid present, well marked alisphenoid canal present; braincase low and scarcely domed, lambdoid crest moderately well-developed laterally, low medially; mastoid large, slightly inflated; paraoccipital process small; infraorbital foramen dorsal to P4; antorbital or prelacrimal flange present only as a low ridge; shallow antorbital fossa on anterior surface of zygoma; nasolabialis fossa shallow; maxillary component of zygoma narrow with long, slender posteroventral process ventral to well marked long jugal, slender anterodorsal process of squamosal portion of zygoma overlying jugal; palate with paired maxillary foramina level with P2 and anterior of P3, small paired anterior palatal foramina, lying anterior to the suture between maxilla and palatine; palatal spine absent; basioccipital narrow with ridge in midline, tympanic wing of basioccipital slightly inflated. Mandible with deep, moderately broad coronoid process; mental foramen below p3.

Dental formula: $3/3 \ 1/1 \ 4/4 \ 3/3 = 22$. Dentition robust (see Figs. 1–2). First upper incisor robust, distostyle present; I2 and I3 sub-triangular, anteroflexed, distostyle present. I3 approximately half size of I2; C with anterior basal cusp and distostyle and two roots; P1 and P2 subequal in height, P2 longer than P1, both with anterior basal cusp and distostyle, P1 with two fused roots, P2 with two roots; P3 large, subequal in height to C, lingual cusp (protocone according to Gould, 1995) well developed, three roots present; P4, M1 and M2 quadrate in shape, parastyle well developed, metacone present on M1 and M2; M3 subtriangular in shape, with well developed parastyle and hypocone and metacone distinct in unworn dentition. First lower incisor larger than i2, both semi-procumbent, i2 larger than i3, which is anteroflexed with hypoconulid present; c anteroflexed, greater in height than i3 and p1; p1 and p2 subequal in height and both with a single root; p3 larger with two roots; p4 with well developed paraconid and talonid; m1–m3 with well developed paraconids, m3 less than half size of m1.

ETYMOLOGY

The name of the new species is derived from the Greek μέγας (megas), large; ὅτος (otos), ear; the ears are large in comparison with those of other species of *Hylomys*.

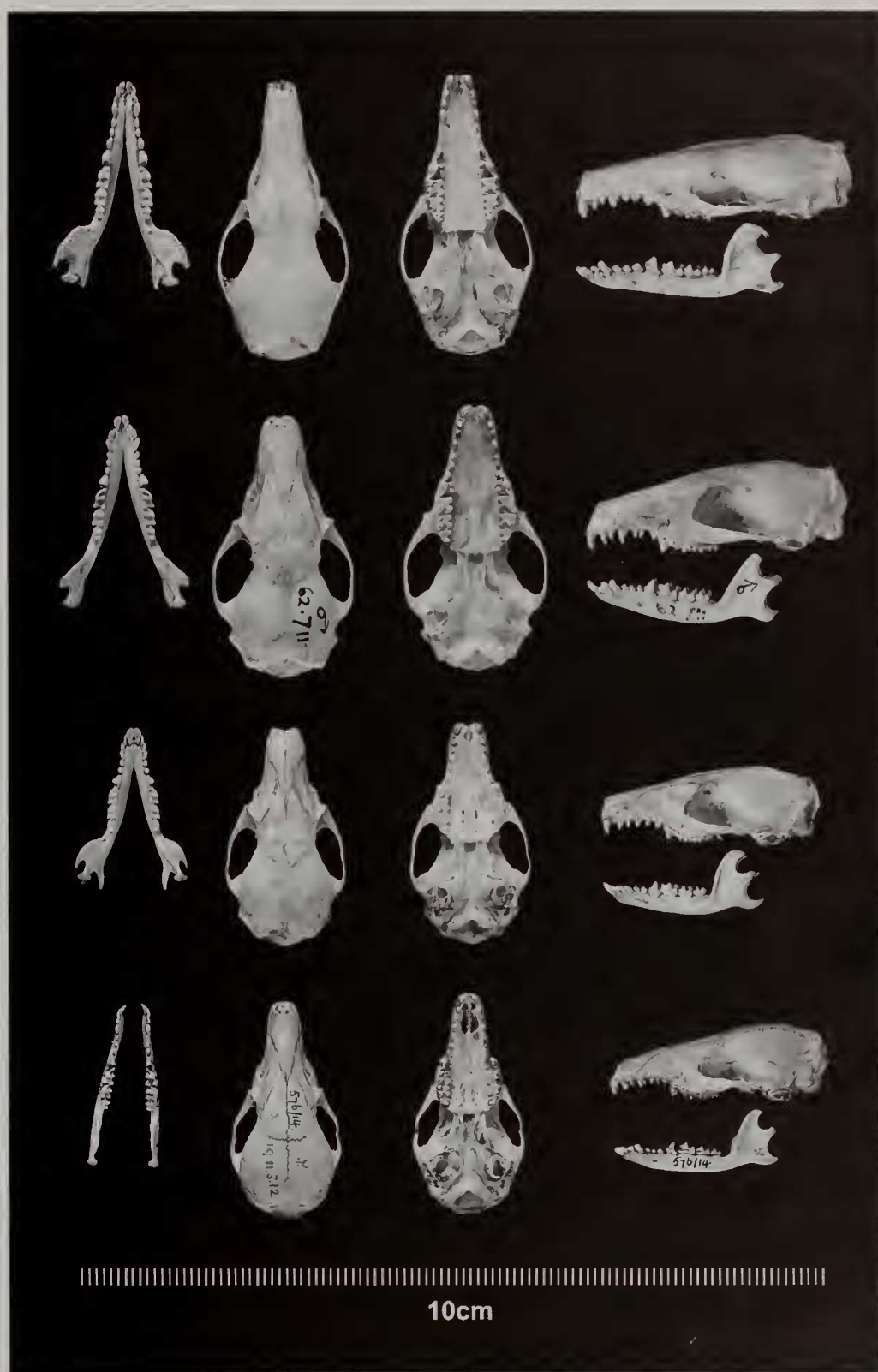


Fig. 1 Crania from left to right of dorsal view of mandible and skull, ventral view of skull, left lateral view of skull and mandible. Top row: *Hylomys megalotis* BMNH 1999.47; second row: *Hylomys suillus* BMNH 1962.711; third row: *Hylomys sinensis* BMNH 1911.2.1.20; fourth row: *Hylomys parvus* BMNH 1919.11.8.12.

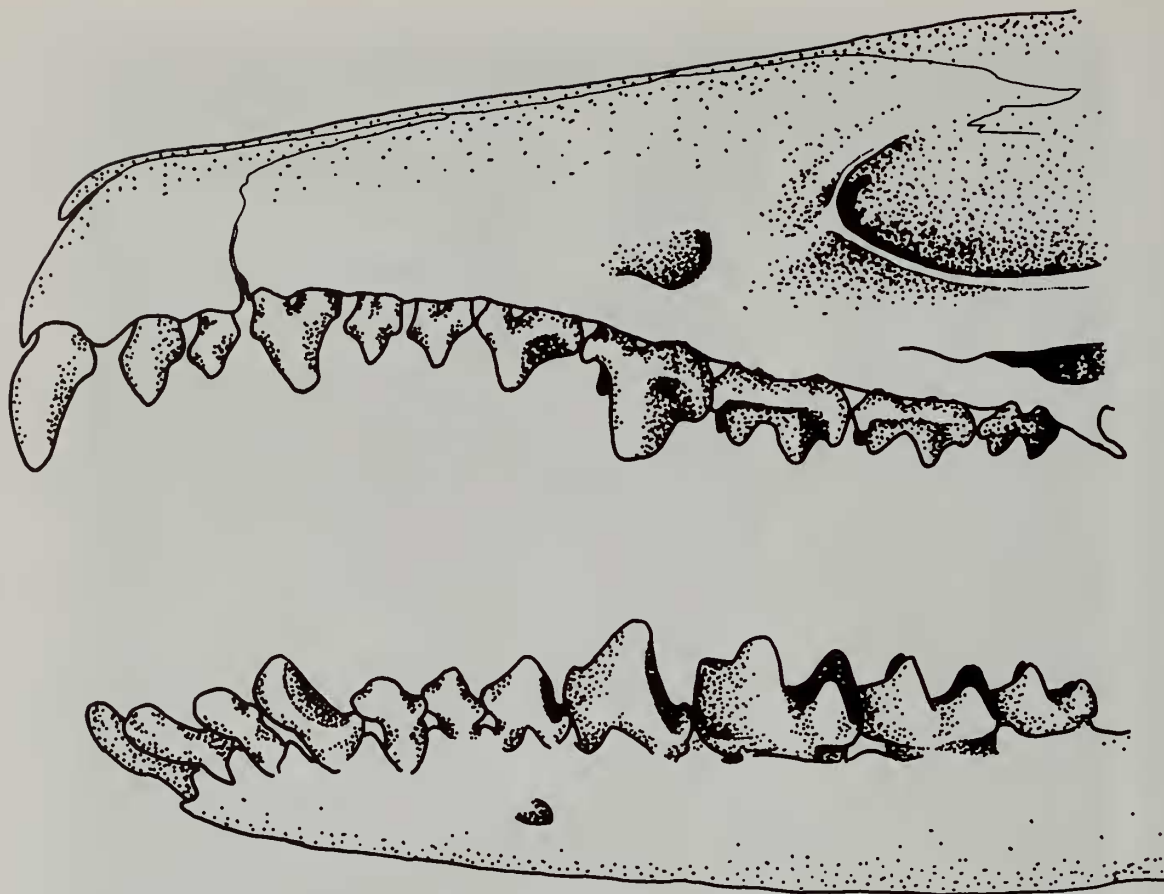


Fig. 2 Lateral view of anterior of skull, mandible and dentition of *Hylomys megalotis* BMNH 1999.44. Scale = 1 mm.

COMPARISON WITH OTHER TAXA

The new species is readily distinguished in external appearance from all other species of *Hylomys*. It is similar in body size but with a considerably longer tail and larger ears (see Table 3). Tail 65–74 % of head and body length in *H. megalotis*, 51–63 % in *H. sinensis*, 27–31 % in *H. hainanensis*, and very short (< 25 %) in *H. parvus* and *H. suillus*. The lack of flattened spinous hairs in the pelage distinguishes *H. megalotis* from *H. suillus* and *H. sinensis*. The rhinarium is more extensive posteriorly than in *H. sinensis* but more elongate and narrower than in *H. suillus*. The claws and first and fifth digits of the forefeet of *H. sinensis*, *H. suillus* and *H. parvus* are not lengthened as in *H. megalotis* and the cheiridia are smaller than in *H. megalotis*. The sole and tarsal region of the hindfoot are naked in *H. megalotis*, differing from the haired soles found in *H. sinensis* and *H. suillus*. The paired pre-anal glands are midway between the cloaca and the anus in *H. sinensis* and close to the anus in *H. suillus*, so differing from that of *H. megalotis*, in which the single opening is positioned immediately posterior to the cloaca.

The skull of *H. megalotis* is more elongate in appearance than any of the other species of *Hylomys*; it is longer, with a longer, narrower rostrum, longer upper tooththrow and the braincase is shallower relative to its breadth (see Fig. 1 and Table 3). The posterodorsal region of the premaxilla is widely separated from the anterodorsal region of the frontal by the maxilla in *H. megalotis*, narrowly separated in *H. hainanensis* but in contact or nearly in contact in *H. sinensis*, *H. suillus* and *H. parvus* (see Table 4). As in *H. sinensis*, but unlike other species of *Hylomys*, the posteriormost

portion of the nasals in the new species extend to the level of the antorbital rim. *Hylomys megalotis* has a shallow antorbital fossa unlike the moderately deep fossa of *H. sinensis* and *H. parvus*, and the deep fossa in *H. suillus*. The zygoma of *H. megalotis* differs from all other species of *Hylomys*: the maxilla is considerably narrower, the nasolabialis fossa shallower and the jugal more extensive. As in *Podogymnura aureospinula* and *Echinosorex*, a distinct posteroventral process is present on the maxillary region of the zygoma of *H. megalotis*, indistinct in *H. parvus* but absent in *H. suillus*, *H. sinensis* and *H. hainanensis*. The supraorbital process of the frontal of *H. megalotis* is poorly defined and blunt, the anterior process of the parietal absent and the parietal is widely separated from the maxilla by the frontal in the supraorbital region, as in *Podogymnura* and *Echinosorex*; in *H. parvus* the supraorbital process of the frontal is poorly defined and blunt but the anterior process of the parietal is short but distinct, narrowly separated from the maxilla by the frontal; in *H. suillus*, *H. hainanensis* and *H. sinensis* the anterior process of the parietal is distinct, scarcely separated from the maxilla and contributing to the well marked supraorbital process of the frontal. The optic and suboptic foramina are well separated in *H. megalotis* but lie close together in *H. suillus*, *H. sinensis* and *H. parvus*. An anteroventral process of the alisphenoid is present in *H. megalotis*, unlike all other *Hylomys* and *Podogymnura*. As in *Podogymnura* and *Echinosorex*, the palatine foramina are small and positioned anterior to the maxillary/palatine suture in *H. megalotis* and long grooves for the palatine artery are present in the palate, whereas the elongated palatine foramina in other species of *Hylomys* lie at the maxillary/

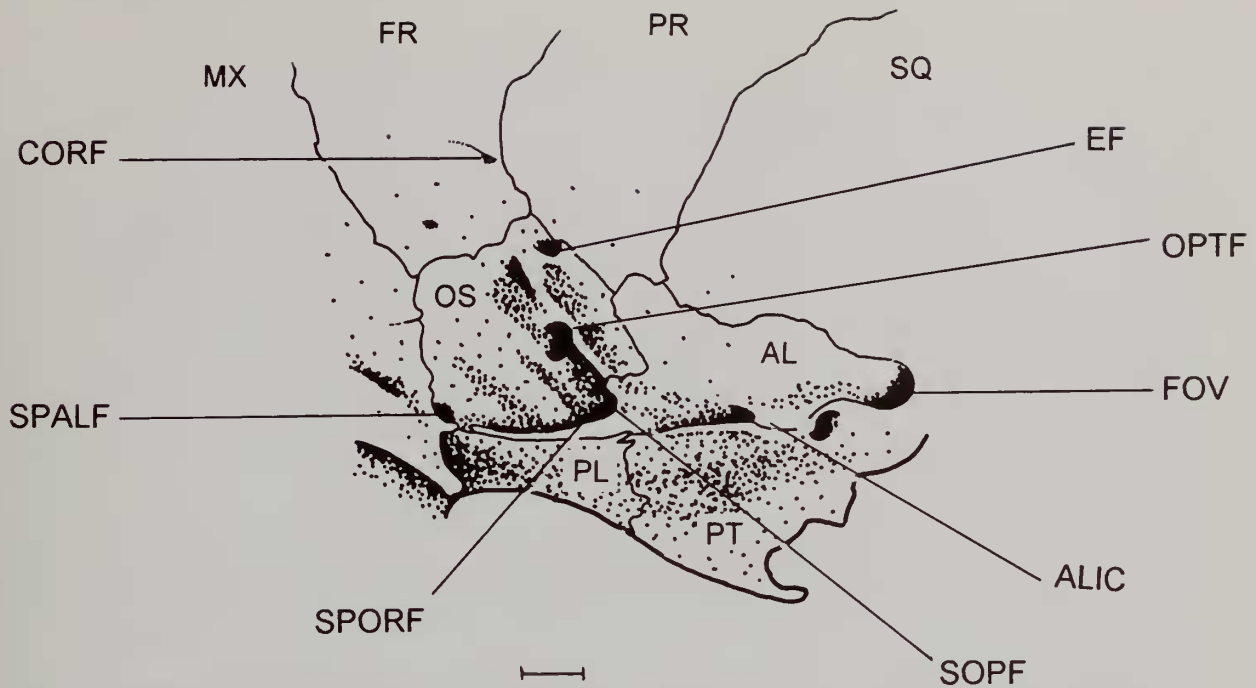


Fig. 3 Lateral view of left orbital region of *Hylomys megalotis* BMNH 1999.44. Scale = 1 mm. Abbreviations: AL – alisphenoid, ALIC – alisphenoid canal, CORF – cranio-orbital foramen, EF – ethmoid foramen, FOV – foramen ovale, FR – frontal, MX – maxilla, OPTF – optic foramen, OS – orbitosphenoid, PL – palatal, PR – parietal, PT – pterygoid, SPOPF – suboptic foramen, SPALF – sphenopalatine foramen, SPORF – sphenorbital foramen, SQ – squamosal.

palatine suture and the palatine artery grooves are small or indistinct. The anterior opening of infraorbital canal is dorsal to P3/P4 in most species of *Hylomys* but dorsal to P4/M1 in *H. megalotis*, *H. parvus* and *Echinosorex*, and yet more posteriorly positioned in *Podogymnura*.

The dentition of *H. megalotis* is considerably more robust than that of any of the other species of *Hylomys*. The dental formula is the same as in *H. suillus* and *H. parvus* and these species are distinguished from *H. hainanensis*, which lacks p1 and *H. sinensis*, which lacks P1 and p1. In *H. megalotis* and *H. parvus*, P2 has two roots, unlike the other species which have either one or two well fused roots. Unlike all other species which lack a lingual cusp, P3 of *H. megalotis* has a well developed lingual cusp as in *Echinosorex*, and this tooth is large with three roots as in *Podogymnura* and *Echinosorex*; p3 is larger than p2 with two roots as in *H. parvus*, *Podogymnura* and *Echinosorex*, while p3 is slightly smaller than p2 with one root in *H. suillus*, *H. sinensis* and *H. hainanensis*.

RESULTS OF THE PHYLOGENETIC ANALYSIS

Forty equally most parsimonious trees were retained in the branch and bound analysis, 141 steps in length, with a Consistency Index of 0.72, Retention Index of 0.93 and Rescaled Consistency Index of 0.66. In all most parsimonious trees the two subfamilies, Galericinae and Erinaceinae, readily segregated and the Galericinae further separated into two distinct groups: a clade comprising *Echinosorex* and *Podogymnura*, the other clade confined to *Hylomys*. Most of the variation found among all trees occurred within the Erinaceinae, since for the Galericinae twenty of the trees showed the configura-

tion seen in Fig. 4a, while the remaining trees all showed the alternative arrangement for this subfamily (Fig. 4b). That part of the tree obtained by Frost *et al.* (1991: Fig.9) for the Galericinae is illustrated as part of Fig. 4a. The strict consensus tree (see Fig. 5) revealed strong bootstrap support (97%) for the Galericinae and for a clade of *H. suillus*, *H. sinensis* and *H. hainanensis*, and this tritomy also had a high Bremer support index. There was moderate bootstrap support (83%) for a clade of *H. suillus*, *H. sinensis*, *H. hainanensis* and *H. parvus*, and a clade comprising all species in the genus *Hylomys* occurred in 77% of the replicates. The bootstrap support value for a clade of *Echinosorex* and *Podogymnura* was low at only 64%. Within the genus *Hylomys*, *H. megalotis* was basal to all other species. Clades with bootstrap support values less than 50%, respectively of *H. sinensis* and *H. hainanensis* (42%), and *H. suillus* and *H. hainanensis* (43%) were considered to be unresolved.

The shared derived character transformations (synapomorphies) which were revealed by the analysis are recorded below, using the format of character number quoted from Frost *et al.* (1991) followed by character transformation state, where (0) equals the ancestral and (1) the derived character state.

SYNAPOMORPHIES OF GALERICINAE:

[8.1] Antorbital or pre-lacrimal flange: (0) not developed, lacrimal canal visible in lateral view; (1) developed so that the lacrimal canal is obscured in lateral view. CI 1.000.

[10.2] Jugal size; (0) large, reaches lacrimal; (1) small, does not reach lacrimal; (2) vestigial, confined to lateral rim of zygoma; (3) absent. In ACCTRAN the transformation was from 1 → 2, in DELTRAN the change was from 3 → 2. CI 1.000.

[62.1] P4 lingual roots: (0) one; (1) two unfused; (2) two fused. CI 1.000. This state occurs in all Galericinae but was shown only in DELTRAN.

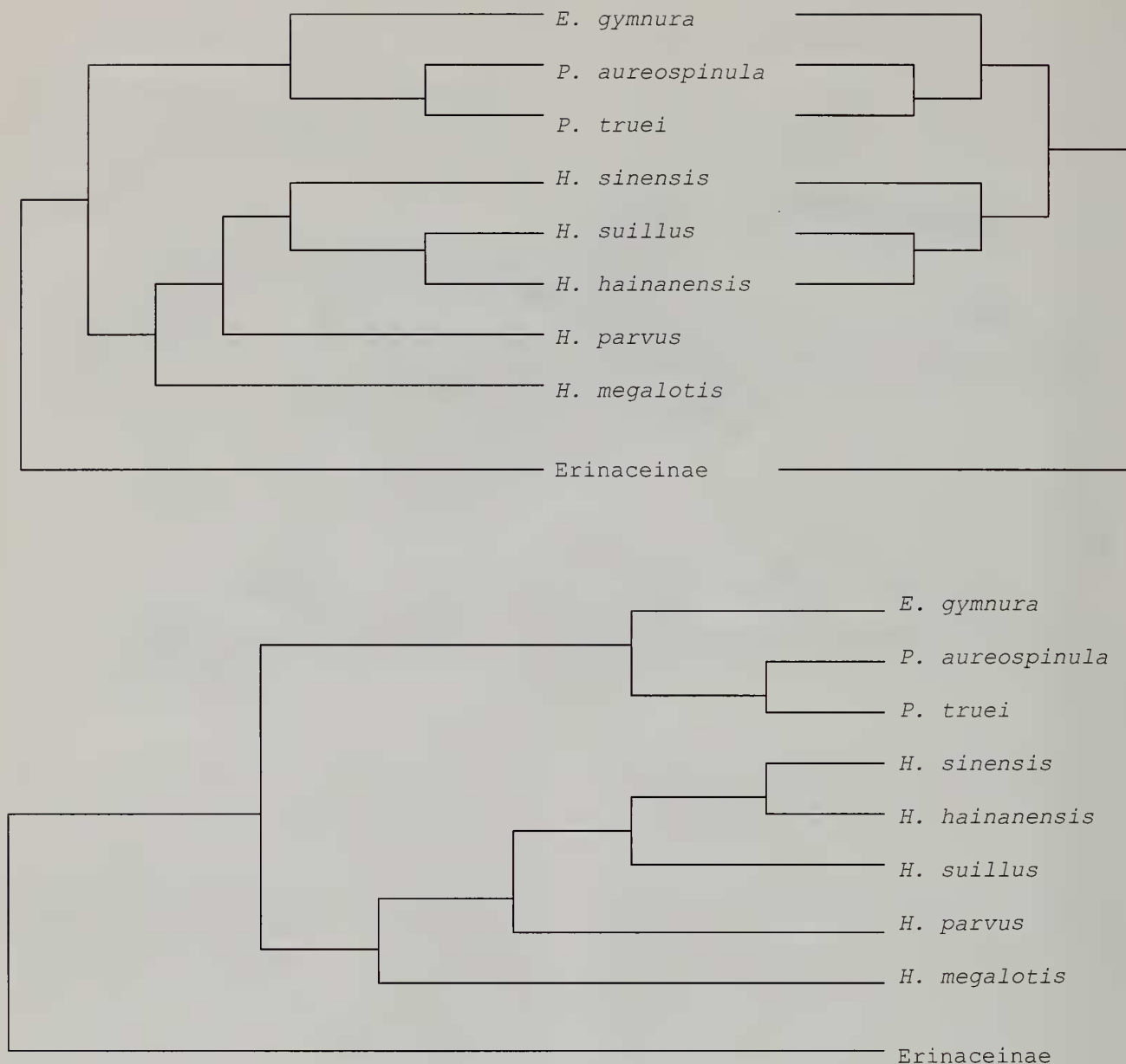


Fig. 4 Comparison of trees obtained for the Galericinae. (a) One of twenty most parsimonious trees, all showing the same configuration for the Galericinae. Tree length 141 steps, with a Consistency Index of 0.72, a Retention Index of 0.93, and a Rescaled Consistency index of 0.66. The branching pattern on the left shows the results from the analysis of this study, that on the right is partially redrawn from Frost *et al.* (1991: fig. 9), restricted to show only the relationships within the Galericinae and is 128 steps in length with a Consistency Index of 0.76. (b) One of the remaining twenty most parsimonious trees, showing the alternate arrangement for the Galericinae.

[66.1] M3 hypocone (see Frost *et al.* 1991) or metastylar spur (see Gould, 1995): (0) absent or weak; (1) present, well developed on buccal side. CI 1.000.

[69.1] Axis, posteroventral keel: (0) absent; (1) present. CI 1.000.

[71.1] Scapula, metacromium process: (0) deltoid, amorphous projection; (1) long, fusiform projection. CI 1.000.

[72.1] Sacral vertebrae, neural spines: (0) not fused into continuous longitudinal plate; (1) fused into continuous longitudinal plate. CI 1.000.

[73.1] Ischium, posterodorsal process (see Gould, 1995 for correction of error by Frost *et al.* 1991): (0) not greatly elongated; (1) greatly elongated. CI 1.000.

[74.1] Tibia, lateral flange on antero-superior margin: (0) absent or weakly present; (1) strongly developed. CI 1.000.

SYNAPOMORPHY OF *HYLOMYS*:

[19.1] Cranio-orbital foramen in the frontal: (0) closely associated or joined with the ethmoid foramen; (1) foramina widely separated. The terminology for this character is confusing. Frost *et al.* (1991) used the name ophthalmic foramen (which they attributed to Butler (1948) although this name could not be found in this paper), but Gould (1995: character 19) pointed out that this foramen had been misidentified by Butler and is the anterior opening for the superior ramus of the stapedia artery. Gould also referred to this foramen as

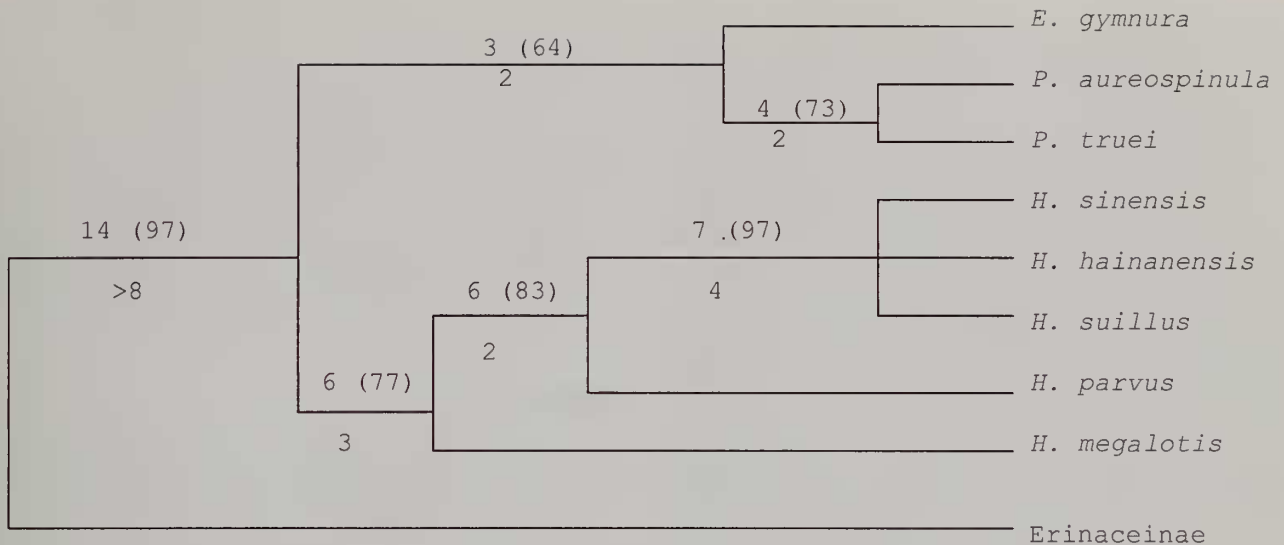


Fig. 5 Strict consensus of 40 most parsimonious trees. The branch lengths are shown above the branches followed by the bootstrap support values in parentheses, representing the percentage of trees containing the specified clades. The Bremer support indices are given below the branches.

the sphenofrontal foramen and McDowell (1958) as the sinus canal. CI 1.000.

SYNAPOMORPHY OF *HYLOMYS SINENSIS*, *H. HAINANENSIS*, *H. SUILLUS* AND *H. PARVUS*:

[4.1] Size of palatal foramina: (0) small; (1) anterior foramina elongated posteriorly; (2) anterior foramina elongated to include middle palatine foramina. CI 1.000.

SYNAPOMORPHIES OF *HYLOMYS SINENSIS*, *H. HAINANENSIS*, *H. SUILLUS*:

[13.1] Supraorbital process of frontal on parietal/frontal suture: (0) absent or poorly defined; (1) sharp, well defined. CI 1.000.

[16.1] Anterior process of parietal: (0) absent or very weak; (1) extends anteriorly along the supraorbital rim to form the base of the supraorbital process. CI 1.000.

[57.1] p3: (0) two roots present, larger in size than p2; (1) one root present, nearly equal in size to p2; (2) absent. CI 1.000.

The analysis found no autapomorphic characters to define *H. megalotis* but the following apomorphies for this species are recorded as follows:

[1.1] Posteriormost extension of nasals: (0) anterior to the level of the antorbital rim; (1) medial or posterior to the level of the antorbital rim. CI 0.333. Homoplasious with *H. sinensis* but also with Erinaceinae.

[5.1] Location of the anterior palatine foramina: (0) at the maxilla/palatine suture; (1) anterior to the maxilla/palatine suture. CI 0.500. Shown only in DELTRAN, homoplasious with *Echinosorex* and *Podogymnura*.

[17.1] Anterior process of alisphenoid: (0) absent; (1) present. CI 0.500. Homoplasious with Erinaceinae. This character, defined as a narrow, fusiform anterior process of the orbital wing of the alisphenoid is, according to Frost *et al.* (1991), related to the location of the sphenopalatine foramen and involved with shortening of the orbitotemporal region. Gould (1995) commented that the relative position of the suboptic foramen (her character 21 scored thus: (0) anterior to the sphenorbital fissure; (1) present in the medial wall of the sphenorbital fissure; (2) present in the medial wall of the sphenorbital fissure but hidden within the fissure) seems to be

related to the shortening of the skull in erinaceids. As the skull shortens, the alisphenoid overlaps the orbitosphenoid, creating a strong alisphenoid wing [character 17 of Frost *et al.* (1991) and Gould (1995)], the degree of overlap seems to be directly related to the visibility of the suboptic foramen from lateral view and, as pointed out by Butler (1948) the orbitosphenoid is reduced in size. While the alisphenoid is more extensive in *H. megalotis* than in other galericines, and the suboptic and sphenorbital foramina are partially concealed in lateral view, the orbitotemporal region is not obviously shortened. The anterior process in *H. megalotis* is fully ventral in location and is actually or nearly in contact with a short posteroventral process of the maxilla, thus contributing to the ventral floor of the orbit, however the orbitosphenoid is not reduced in size. It is possible that this character state in *H. megalotis* is not homologous with that of the Erinaceinae and that it actually represents a separate character transformation, alternatively it is scored incorrectly and the plesiomorphous condition should be the presence of the anterior process.

[22.1] Palatal shelf and spine: (0) well developed spine on posterior palatal shelf; (1) spine absent or vestigial. CI 0.200. Shown only in DELTRAN, homoplasious with *Podogymnura*, *H. parvus*, and *Atelerix*.

DISCUSSION

The addition of two taxa to the analysis performed by Frost *et al.* (1991) provided broadly similar results in that the Galericinae divided into two main groups: one comprising *Echinosorex* and *Podogymnura*, the second including all five species of *Hylomys*. The results of the current phylogenetic analysis lend support to the taxonomy proposed by Frost *et al.* (1991) that the three species of *Hylomys* considered in their analysis (*H. suillus*, *H. sinensis* and *H. hainanensis*) are correctly attributed to a single genus rather than the three separate genera (respectively *Hylomys*, *Neotetracus* and *Neohylomys*) maintained by Corbet (1988). The additional species of *Hylomys* however, reduced the degree of support for the genus and, on this particular morphological data set, a considerable degree of homoplasy is evident within the *Hylomys* clade. There was only one unique synapomorphy for the

Hylomys clade (character 19.1: the wide separation between the cranio-orbital and ethmoid foramina), two of the other apomorphies (34.1: the inflation of the mastoid region between the exoccipital and the squamosal, and 41.1: the expanded exoccipital) showing homoplasy with *P. truei*, while the third character state (50.1: upper canine slightly larger than the adjacent post-canine teeth) is not shown by *H. sinensis* (50.2: upper canine approximately equal in size to the adjacent post-canine teeth). There are no autapomorphies defining *H. megalotis*, which shows more plesiomorphy than the other species of *Hylomys*; many of its features are homoplasious with *Echinosorex*, *Podogymnura* and *Erinaceinae*.

Hylomys is a morphologically variable genus, containing species that are generally well segregated and show little overlap in species range. *Hylomys hainanensis* is a geographically isolated island form and while *H. sinensis* and *H. parvus* are each parapatric with *H. suillus* in a few areas, Corbet (1988) pointed out that in regions where *H. sinensis* and *H. suillus* occur, *H. sinensis* is found at greater altitudes than *H. suillus*. Similarly Ruedi *et al.* (1994) showed that although *H. parvus* is currently restricted to moss forests at the peak of Gunung Kerinci, Sumatra at greater altitudes than *H. suillus*, the latter occurs elsewhere at greater and lesser altitudes. Both Corbet (1988) and Ruedi *et al.* (1994) invoked ecological factors such as competitive exclusion to explain the altitudinal segregation of these three species, but did not provide data to support this supposition. There are few distribution records of *H. suillus* and *H. megalotis* in Lao PDR, which potentially may be sympatric or possibly parapatric if *H. megalotis* should prove to be ecologically restricted to the specific limestone habitat in which it was first collected.

Little is known about the biology of *Hylomys*. *Hylomys sinensis* is believed to be entirely terrestrial and *H. suillus* mainly so, although this species has also been observed climbing in low bushes (Lekagul & McNeely, 1977). *Hylomys suillus* occurs in hilly or montane humid forests with dense undergrowth. *H. sinensis* in cool damp forests in the cover of runways and under logs and rocks. In their original description Shaw & Wong (1959) reported that *H. hainanensis* spends most of its time in underground burrows and that the cylindrical body, short tail and claws are adaptations to a fossorial life. *Hylomys parvus* is apparently restricted to high altitude moss forest. There is no information about the behavioural ecology of *H. megalotis* but the limestone karst where it has been found to date is an unusual habitat and some of the morphological features of this species, such as the moderately broad forefeet with long, fairly stout claws, the long naked hindfeet with large cheiridia, the moderately long tail and the comparatively flattened braincase may be adaptations to life in this habitat.

ACKNOWLEDGEMENTS. We would like to thank the staff of WWF-Thailand, the Lao PDR Department of Forestry (DoF) and the Forest Management and Conservation Project (FOMACOP) for permission to work in Lao PDR and for organising the project; in particular Bouahong Phanthanousy (National Project Director, FOMACOP), Bouaphanh Phantavong (Deputy National Project Director, FOMACOP), Robert Mather and Robert Steinmetz (WWF-Thailand) and Bruce Jefferies (FOMACOP), who additionally oversaw the export of specimens. We are very grateful to Maurice Webber for his vital contribution to all aspects of the fieldwork.

Assistance in the field was gratefully received from Thongphanh Ratanalangsy (Khammouan Limestone and DongPhu Vieng NBCA Co-ordinator), Sinnasone Seangchanthanarong (DoF) and Nousine Latvylay (driver for FOMACOP in Savannakhet). The headmen and villagers from Pontong, Muang, Mouangkhai, Louang, Vieng, Kengkhot, Thamtem and Tonglom provided excellent field support and companionship, and without them this project would not have been possible. We would like to thank Angela L. Smith for her help in measuring specimens at TISTR and for her comments on the manuscript.

Field work was funded by the Global Environment Facility through the World Bank to the Government of Lao PDR, via a contract with Burapha Development Consultants, sub-contracted to WWF-Thailand.

We thank Bob Randal (AMNH), Jacques Cuisin (MNHN) and Nivesh Nadee (TISTR) for making specimens in their collections available to us. We are very grateful to Andrew Cabrinovic (NHM) for specimen preparation, to Harry Taylor, Photographic Unit (NHM) for the excellent photographs and to Karen Fisher (volunteer, NHM) for her kind assistance with documentation.

We are grateful to Dr François Catzeflis, Institut des Sciences de l'Evolution, Université Montpellier for his constructive review of the manuscript. We particularly thank Dr Darrell Siebert, NHM for his generous guidance with the phylogenetic analysis and constructive criticism of the manuscript.

REFERENCES

- Blainville, H. M. D. de 1838. Recherches sur l'ancienneté des Mammifères insectivores à la surface de la terre; précédées de l'histoire de la science à ce sujet, des principes de leur classification et de leur distribution géographique actuelle. *Compte Rendus Hebdomodaires de Séances de l'Académie des Sciences* 6: 738–744.
- Butler, P. M. 1948. On the evolution of the skull and teeth in the Erinaceidae, with special reference to fossil material in the British Museum. *Proceedings of the Zoological Society, London* 118 (2): 446–500.
- Corbet, G. B. 1988. The family Erinaceidae: a synthesis of its taxonomy, phylogeny, ecology and zoogeography. *Mammal Review* 18 (3): 117–172.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Frost, D. R., Wozencraft, W. C. & Hoffmann, R. S. 1991. Phylogenetic relationships of hedgehogs and gymnures (Mammalia: Insectivora: Erinaceidae). *Smithsonian Contributions to Zoology* (518): 1–69, 19 plates.
- Gould, G. C. 1995. Hedgehog phylogeny (Mammalia, Erinaceidae) – the reciprocal illumination of the quick and the dead. *American Museum Novitates* (3131): 1–45.
- Kitching, I. J., Forey, P. L., Humphries, C. J. & Williams, D. M. 1998. *Cladistics. Second edition. The theory and practice of parsimony analysis*. Oxford University Press, Oxford, New York, Tokyo.
- Lekagul, B. & McNeely, J. A. 1977. *Mammals of Thailand*. Kurusapha Ladprao Press, Bangkok.
- McDowell, S. B. 1958. The greater Antillean insectivores. *Bulletin of the American Museum of Natural History* 115 (3): 117–214.
- McKenna, M. C. & Bell, S. K. 1997. *Classification of mammals above the species level*. Columbia University Press, New York.
- Mearns, E. A. 1905. Descriptions of new genera and species of mammals from the Philippine Islands. *Proceedings of the United States National Museum* 28: 425–460.
- Müller, S. 1840. Over de Zoogdieren van den Indischen Archipel (No. 2) pp. 9–57. In C. J. Temminck (ed.) *Verhandelingen over de Natuurlijke Geschiedenis der Nederlandsche overzeesche bezittingen, door de Leden der Natuurkundige commissie in Indië en andere Schrijvers*. A. Arnz & Co., Leiden.
- Novacek, M. J. 1986. The skull of lepidic insectivorans and the higher-level classification of eutherian mammals. *Bulletin of the American Museum of Natural History* 183 (1): 1–111.
- Osgood, W. H. 1932. Mammals of the Kelley-Roosevelts and Delacour Asiatic expeditions. *Publications of the Field Museum of Natural History, Zoology* (18): 193–339.
- Raffles, T. S. 1822. Descriptive catalogue of a zoological collection, made on account of the Honourable East India Company, in the island of Sumatra and its vicinity, under the direction of Sir Thomas Stamford Raffles, Lieutenant-Governor of Fort Marlborough; with additional notices illustrative of the Natural History of these countries. *Transactions of the Linnean Society, London* 13 (1): 239–274.
- Robinson, H. C. & Kloss, C. B. 1916. Preliminary diagnoses of some new species and subspecies of mammals and birds obtained in Korinchi, West Sumatra, Feb.–June 1914. *Journal of the Straits Branch of the Royal Asiatic Society* (73): 269–278.
- Robinson, M. F. 1999. Order Insectivora, pp. 221–223 In J. W. Duckworth, R. E. Salter & Khounboline, K. (compilers) *Wildlife in Lao PDR 1999 status report*. IUCN, Vientiane.
- Ruedi, M., Chapusiat, M. & Iskander, D. 1994. Taxonomic status of *Hylomys parvus* and *Hylomys suillus* (Insectivora: Erinaceidae): biochemical and morphological analyses. *Journal of Mammalogy* 75 (4): 965–978.
- Swofford, D. L. 1999. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland, Massachusetts.
- Shaw, T. H. & Wong Song 1959. [A new Insectivore from Hainan]. *Acta Zoologica Sinica* 11: 422–425. [In Chinese; English summary].
- Trouessart, E.-L. 1909. *Neotetracus sinensis*, a new insectivore of the family Erinaceidae. *Annals and Magazine of Natural History* (8) 4: 389–391.

Table 1 Comparative material*Hylomys sinensis*

BMNH 1932.4.19.3 Chapa, Tonkin, [Vietnam]
 BMNH 1933.4.1.117–134 Chapa, Tonkin, [Vietnam]
 BMNH 1933.4.1.536–541 Chapa, Tonkin, [Vietnam]
 BMNH 1911.2.1.15–23 Omi-san, Omi-Hsien, S. Szechwan [Sichuan, PDR China]
 BMNH 1982.205 Omi-san, Omi-Hsien, S. Szechwan [Sichuan, PDR China]
 MNHN 1911–1180–1184 Ta-Tsien-Lou, Setchouen [Sichuan, PDR China]
 BMNH 1909. 12.13.1 Ta-Tsien-Lou, Szechuan [Sichuan, PDR China]
 BMNH 1911.8.6.1 Yengyuek, Yunnan, [PDR China]
 BMNH 1912.7.15.1 Ching-tsai-Yang, Yunnan, [PDR China]
 BMNH 1914.10.23.3 Near Yang-fsi, W. Yunnan, [PDR China]

Hylomys suillus

BMNH 1909.7.20.2–3 Sima, Burma [Myanmar]
 AMNH 44112 Nam-Ting, Yunnan, China [PDR China]
 BMNH 1925.1.1.17 Bao-Ha, Tonkin, [Vietnam]
 BMNH 1926.10.4.42 Xieng-Khouang, Laos [Lao PDR]
 AMNH 87313 Bologens Plateau, Laos [Lao PDR]
 BMNH 1926.10.4.36–41 Dak-to, Annam
 MNHN 1929–320–325 Dak-to, Annam
 BMNH 1955.1422 Tasan, Chumpawn, Peninsular Siam [Thailand]
 TISTR 54-611 Huey Mae Sanam, Chiangmai, Thailand
 TISTR 54-613 Trang, Muang, Chong, Thailand
 TISTR 54-614–615 Khao Yai National Park, Korat, Thailand
 TISTR 54-616 Phu Nam Tok, Saraburi, Thailand
 TISTR 54-617 Pok Nam Tok, 21 km from Saraburi, Saraburi, Thailand
 TISTR 54-618 Mae Sai, B. Santon Poi, Chiang Rai, Thailand
 TISTR 54-1498–1500 Pak Thong Chai, Sakaerat, Nakhon Ratchasima, Thailand
 TISTR 54-1811 Pak Thong Chai, 17 km S of Pak Thong Chai, Nakhon Ratchasima, Thailand
 TISTR 54-1809–1810 Khon San, Pa Phu Khieo, Chaiyaphum, Thailand
 TISTR 54-1812 Phu Kradung National Park, Loei, Thailand
 BMNH 1960.8.4.7 Ulu Langat Forest Reserve, Kajang, Selangor, [Malaysia]
 BMNH 1961.1158 Ulu Langat Forest Reserve, Kajang, Selangor, Malaysia
 BMNH 1955.1420 Semangko Pass, Pahang, Federal Malay States [Malaysia]
 BMNH 1961.1159 Padang, Jeriau, Fraser's Hill, Pahang, Malaysia
 BMNH 1962.710–711 Jandai Baik, Pahang, Malaysia
 BMNH 1912.10.22.7 Pelarit, Perlis, Malay [Malaysia]
 BMNH 1955.1421 Pelarit, Perlis, Federal Malay States [Malaysia]

BMNH 1912.10.22.8 Perlis, Malay Peninsula [Malaysia]
 BMNH 1955.1423 Jor, Batang Pasang, Perak, Federal Malay States [Malaysia]
 BMNH 1955.1424 Kedah Peak, Federal Malay States [Malaysia]
 BMNH 1962.711a Kedah Peak, Kedah, Malaya [Malaysia]
 BMNH 1892.9.6.4 Mt. Kina Balu [Malaysia]
 BMNH 1895.10.4.3–4 Mt. Kina Balu [Malaysia]
 BMNH 1955.661 Mount Kinabalu, British North Borneo [Malaysia]
 BMNH 1971.2614–2615 Mt. Kinabalu, N Borneo [Malaysia]
 MNHN 1889-37 Mont Kina Balu, Borneo [Malaysia]
 MNHN 1893-132–133 Mont Kina Balu, Borneo [Malaysia]
 BMNH 1971.2616 Dusan Dankulum, Kinabalu, N Borneo [Malaysia]
 BMNH 1971.2617–2618 Tinampoh, Bundu Tuhau rest house, N Borneo [Malaysia]
 BMNH 1919.11.5.7 Korinchi, Sumatra [Sumatera, Indonesia]
 AMNH 102532 Seletan, Mocamh Doewa, Sumatra [Sumatera, Indonesia]
 AMNH 102533 Seletan, Mocamh Doewa, Sumatra [Sumatera, Indonesia]
 AMNH 102534 Seletan, Mocamh Doewa, Sumatra [Sumatera, Indonesia]
 AMNH 102820 Lampung, Kalianda, Sumatra [Sumatera, Indonesia]
 BMNH 1954.45 Tjibodas, West Java [Jawa, Indonesia]
 BMNH 1954.46–48 Sodong Jerok, Idjen Massif, East Java [Jawa, Indonesia]
 BMNH 1961.1743 Tjemorosewu, Mt. Lawu, Java [Jawa, Indonesia]
 AMNH 106111 Java [Jawa, Indonesia]

Hylomys parvus

BMNH 1919.11.5.8–12 Korinchi, Sumatra [Sumatera, Indonesia]

Podogymnura truei

BMNH 1953.659–660 Baclayan, E slopes of Mount Apo, Mindanao, Philippine Islands

Echinosorex gymnura

BMNH 1914.12.8.101–104 Bankachon, Tenasserim [Myanmar]
 BMNH 1955.1452 Changkat Mentri, Perak, Federal Malay States [Malaysia]
 BMNH 1955.1453 Damansara Road, Kuala Lumpur, Selangor, Federal Malay States [Malaysia]
 BMNH 1961.1156 Rontau Panjang, Klang, Selangor, Malaya [Malaysia]
 BMNH 1961.1157 Sungei Buloh, Selangor, Malaya [Malaysia]
 BMNH 1961.1157 Sungei Buloh, Selangor, Malaya [Malaysia]
 BMNH 1951.179–180 Mount Dulit, Sarawak, Borneo [Malaysia]
 BMNH 1951.181 Tinjar River, Baram District, Sarawak, Borneo [Malaysia]
 BMNH 1971.2613 12 miles N of Kalabakan, Tawau, N Borneo [Malaysia]

Table 4 Summary of comparative cranial and dental characters of the subfamily Galericinae

Character	<i>Hylomys sinensis</i>	<i>Hylomys hainanensis</i>	<i>Hylomys sullus</i>	<i>Hylomys parvus</i>	<i>Hylomys megalotis</i>	<i>Podogymnura</i>	<i>Echinosorex</i>
Postero-dorsal region of premaxilla relative to antero-dorsal region of frontal	More or less in contact	Narrowly separated by maxilla	More or less in contact	More or less in contact	Widely separated by maxilla	Widely separated by maxilla	Nearly in contact
Posterior-most portion of nasals relative to level of antorbital rim	Level	Anterior	Anterior	Anterior	Level	Anterior	Anterior
Antorbital fossa	Moderately deep	Moderately deep	Deep	Moderately deep	Shallow	Shallow	Absent
Zygoma: maxilla	Broad	Broad	Broad	Broad	Narrow	Moderately broad	Intermediate
posteroventral process on maxilla	Absent	Absent	Absent	Indistinct	Distinct	Indistinct / distinct	Indistinct
nasolabialis fossa	Deep	?	Deep	Deep	Distinct, shallow	Distinct, shallow	Indistinct
jugal	Small	?	Small	Small	Extensive	?	Small
Supraorbital process of frontal	Well developed	Well developed	Well developed	Poorly defined, blunt	Poorly defined, blunt	Absent	Absent or poorly defined
Anterior process of parietal	Well developed, contributes to supraorbital process	Well developed, contributes to supraorbital process	Well developed, contributes to supraorbital process	Short, distinct	Absent	Absent	Absent
Width of frontal separating maxilla from parietal in supraorbital region	Very narrow	Very narrow	Very narrow	Narrow	Wide	Wide	Wide
Optic and suboptic foramina	Close together	?	Close together	Close together	Well separated	Close together	Well separated
Cranio-orbital and ethmoid foramina	Widely separated	Widely separated	Widely separated	Widely separated	Widely separated	Joined or closely adjacent	Joined or closely adjacent
Anteroventral process of alisphenoid	Absent	Absent	Absent	Absent	Present	Absent	Absent
Postero-palatine spine	Absent	Present	Present	Absent	Absent	Absent	Present
Palatine foramina: size	Elongated	Elongated	Elongated	Elongated	Small	Small	Small
position relative to maxillary / palatine suture	On suture	On suture	On suture	On suture	Anterior	Anterior	Anterior
Palatine artery grooves	Small or indistinct	Small or indistinct	Small or indistinct	Small or indistinct	Long	Long	Long
Anterior opening of infraorbital canal	Dorsal to P3/P4	Dorsal to P3/P4	Dorsal to P3/P4	Dorsal to P4/M1	Dorsal to P4/M1	Dorsal to P4/M1	Dorsal to P4/M1
C1 size relative to adjacent post-canine teeth	Subequal	Slightly larger	Slightly larger	Slightly larger	Slightly larger	Slightly larger	Significantly larger
p1	Absent	Present	Present	Present	Present	Absent	Present
p2	Absent	Absent	1 or 2 well fused	2	2	1 or 2 well fused	1 or 2 well fused
P3 roots	1 or 2 well fused	1 or 2 well fused	1 or 2 well fused	Absent	Present	Absent	Present
p3 size	Absent	Absent	Absent	Small	Present	Large	Large
p3 roots	Small	Small	Small	Small	Large	Large	Large
p3 size relative to p2	< 3	< 3	< 3	< 3	3	3	3
p3 roots	Slightly smaller	Slightly smaller	Slightly smaller	Larger	Larger	Larger	Larger
	1	1	1	2	2	2	2